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Growth of earthworms (*Allolobophora caliginosa*) in soil mixed with either barley, lucerne or meadow fescue at various stages of decomposition

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With 2 figures

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1. Introduction

Although food availability is a factor of prime importance in controlling earthworm biomass and abundance (SATCHELL 1967), little is known about the food sources of earthworms. Their diet probably varies with the supply of organic matter present in the soil or on the soil surface. The species *Allolobophora caliginosa* SAV. gained mass more rapidly when fed dung than when fed partly decayed leaves or roots of herbage plants (BARLEY 1959) and the palatability of leaves depended on plant species (LINDQVIST 1941). WATERS (1951, 1955) suggested that plant materials must undergo some decomposition by bacteria and fungi before they became usable to the species. He concluded that its main food source consisted of decomposing plant roots. On the other hand, PIEARCE (1978) found roots only occasionally in the ingesta while the majority of recognizable plant remains were fragments of grass leaves and fibrous material. He concluded that *A. caliginosa* fed on well-decomposed detritus.

VAN RHEE (1963) noted that small *Allolobophora* species consumed less organic matter than *Lumbricus terrestris* L. or *Allolobophora longa* UDE, and he suggested that the small species either fed more on microorganisms in the soil or digested their food more completely. Actinomycetes and bacteria in the gut flora of *A. caliginosa* increased greatly in number during passage through the gut (PARLE 1963). The logarithmic increase of the microbial population indicated, according to PARLE (1963), that this increase was caused by bacterial growth and not by the worms selecting bacteria-rich food.

Studies on the diet of *A. caliginosa* have not made clear whether the worms gain nourishment directly from the organic matter or from the microorganisms associated with it, nor is it fully understood how food quality influences earthworm consumption and growth. This study investigates how various origins and decomposition stages of different plant materials influence their nutritional values for juvenile *A. caliginosa*.

Although the species *A. caliginosa* is often placed in the new genus *Aporrectodea* it will here remain in the genus *Allolobophora* to be consistent with earlier papers by the same author.

2. Materials and methods

2.1. Earthworms

Adult *A. caliginosa* were cultured at 15 °C in a mixture of equal volumes of soil and farmyard manure. Every 3 weeks cocoons were collected by wetsieving. They were stored in soil at 5 °C until a sufficient number was obtained and thereafter hatched at 20 °C. Juvenile earthworms of similar masses were used for the experiment according to the technique of LOFS-HOLMIN (1980).

2.2. Preparation of plant materials

Meadow fescue (*Festuca pratensis* L.), barley (*Hordeum distichum* L.) and lucerne (*Medicago sativa* L.) were grown in the field. Meadow fescue and barley were fertilized with 120 kg N ha^{-1} while lucerne received no nitrogen fertilizer. The meadow fescue was harvested before stem elongation, lucerne before flowering and barley after maturing. The ripe ears of barley were excluded. The plant materials were put in separate bags made of jute cloth and buried 15 cm deep in a sandy soil, which was watered during periods of dry weather. The jute cloth allowed soil microorganisms and soil fauna to enter and leave the plant materials. After either one or 3 months, the bags were dug up and the plant materials were washed free from soil, dried at 50 °C and ground in a plant mill to a particle size < 1 mm. Fresh plant materials were dried and ground in the same way.

2.3. Analysis of plant materials

The amount of Kjeldahl N was determined, and the ash content was calculated after combustion of the materials at 600 °C for 6 h. The amount of total C was calculated through combustion of the materials in an O_2-rich environment at 1,400 °C. The difference in thermal conductivity between O_2 and CO_2, which is proportional to the content of total C, was then determined. Samples were also filtered through a 0.5-mm sieve, and the 2 fractions (<0.5 and >0.5 mm) were weighed. The lengths of the particles were measured under a stereo microscope.

2.4. Experimental design

Two grams of each plant material were mixed in pots with 250 g loam soil sieved to 2 mm. The soil *p*H was 6.3 and the carbon and nitrogen contents were 2.2 and 0.23% of dry mass, respectively (STEEN *et al.* 1984). The water content in the mixture was 30% of dry mass and each treatment had five replicates. Since a fresh mixture of lucerne and soil is toxic to *A. caliginosa* (BOSTRÖM & LOFS-HOLMIN 1986) the pots were incubated at 20 °C for two weeks prior to use.

One newly hatched *A. caliginosa* was placed in each pot. The pots were covered with perforated lids, preventing earthworms from escaping while permiting ventilation. Pots were stored in the dark at 15 °C and moistened to keep the water content constant. The worms were weighed regularly, without first voiding them, as long as at least three of the worms in a treatment were active, i.e., had not entered aestivation. The earthworms were given a limited supply of food (2 g) to accentuate the influence of decomposition on growth.

The Gompertz growth equation (FRANCE & THORNLEY 1984) was fitted to the collected earthworm mass data:

$$M = M_0 \cdot e(\mu_0(1 - e^{-Dt})/D) \tag{1}$$

where t = time
M = live mass
M_0 = live mass at time t = 0
μ_0 = the value of the relative growth rate (μ) at time t = 0
D = a parameter describing the decay in the relative growth rate.

The change with time in the relative growth rate was calculated according to:

$$\mu = \mu_0 \cdot e^{-Dt} \tag{2}$$

The model was fitted using the non-linear regression procedure NLIN (SAS Institute Inc. 1982) where μ and D are model parameters. The model does not consider mortality or negative growth rates (e.g. starvation), hence only periods of net increases in earthworm mass were included. Two worms in undecomposed barley and meadow fescue were characterized as abnormal, since their initial masses were unchanged throughout the experiment; they were for that reason excluded from the calculations. Aestivating worms were included since aestivation was probably induced by properties of the plant materials.

The part of the growth curve with the steepest slope was divided into 2 equal time periods and absolute growth rates of earthworms (absolute mass increase per day) during period 1 (days 1—64) and period 2 (days 64—127) were calculated for each material. The maximum earthworm mass gain was calculated for each plant material as the measured maximum mass of each individual worm minus its initial mass.

The preparation resulted in 9 plant materials. Although no material was "undecomposed" in a proper sense when the study started, since all mixtures of soil and plant material were incubated at 20 °C for 2 weeks before the worms were added, the plant material not buried below ground will be referred to as undecomposed. Undecomposed barley, lucerne and meadow fescue will be called B0, L0 and Mf0, respectively. The numerical character indicates the number of months plant materials were below ground.

3. Results

The nitrogen concentrations in meadow fescue and barley increased during decomposition while the C/N ratio decreased (Table 1). In lucerne the nitrogen concentration decreased

Table 1. Concentration (% of d.m. ± S.E.) of ash, Kjeldahl N, total C and C/N ratio in meadow fescue (Mf), lucerne (L) or barley (B) in various stages of decomposition

Material	Ash	Kjeldahl N	Total C	C/N
Meadow fescue				
Mf0	13.1 ± 0.3	1.66 ± 0.00	41.5 ± 0.0	25.0
Mf1	10.7 ± 0.1	2.24 ± 0.01	38.4 ± 0.4	17.1
Mf3	12.7 ± 0.4	2.40 ± 0.01	37.8 ± 0.4	15.8
Lucerne				
L0	7.4 ± 0.1	3.97 ± 0.04	44.7 ± 0.2	11.3
L1	3.1 ± 0.1	2.89 ± 0.04	40.3 ± 0.8	13.9
L3	5.7 ± 1.5	2.17 ± 0.00	43.7 ± 0.2	20.1
Barley				
B0	7.6 ± 0.2	0.67 ± 0.01	43.1 ± 0.2	64.3
B1	5.6 ± 0.4	1.24 ± 0.04	46.3 ± 0.6	37.3
B3	6.1 ± 0.2	1.14 ± 0.02	46.9 ± 0.8	41.1

Note: Figures 0, 1 & 3 indicates the number of months the plant materials were exposed for rotting below ground (N = 2).

Table 2. Mean length (mm) of particles and relative mass of fractions (%) after sieving ground plant materials through a 0.5-mm mesh

Material[1]	Particle length (mm)		Relative mass of particle fraction (%)	
	Particle group (mm)		Particle group (mm)	
	<0.5	>0.5	<0.5	>0.5
Meadow fescue				
Mf0	1.5	2.4	56.4	43.6
Mf1	0.7	1.4	85.3	14.7
Mf3	0.7	1.4	85.0	15.0
Lucerne				
L0	1.2	2.2	43.8	56.2
L1	0.8	1.4	38.1	61.9
L3	0.7	1.2	40.1	59.9
Barley				
B0	1.0	2.8	30.4	69.6
B1	0.8	2.0	29.3	70.7
B3	0.9	1.6	33.7	66.3

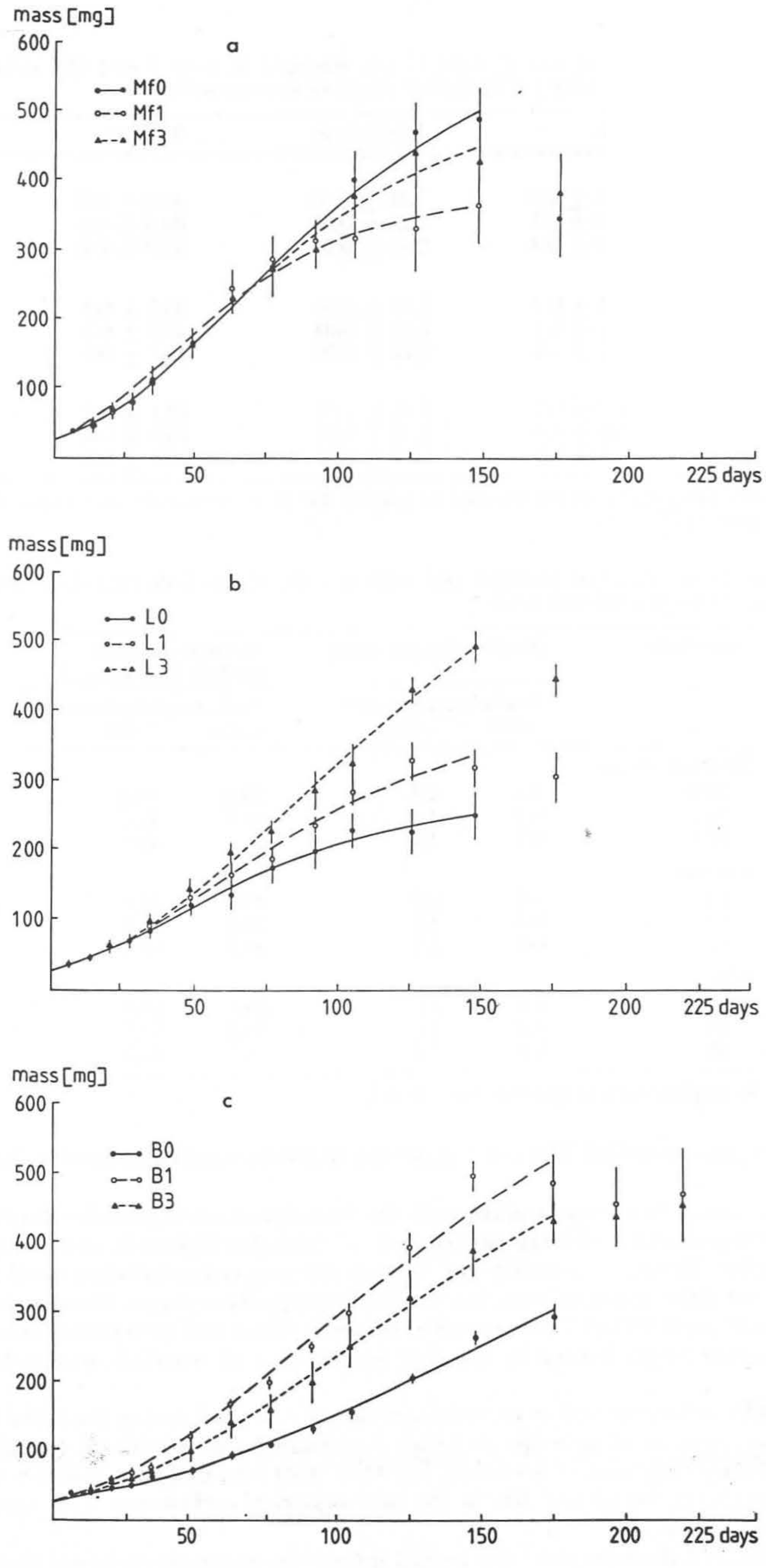
[1] Explanation of symbols see Table 1.

while the C/N ratio increased. The ash content was higher in meadow fescue than in the other materials.

Although ground in the same plant mill, the materials formed particles varying in size and shape. The proportion of small particles ($<$ 0.5 mm) was highest in meadow fescue and lowest in barley (Table 2). In barley and lucerne the proportion between small and large particles did not differ much between the various decomposition stages. However in meadow fescue, the small particle fraction increased in materials which had been buried belowground. The mean particle length formed by grinding decreased in all materials during decomposition.

The juveniles in lucerne and meadow fescue increased in mass during the initial 5 months while the mass increase of juveniles in barley continued for an additional one month (fig. 1a—c). Thereafter their masses decreased and they went into diapause within 6 months in all treatments except for B1 and B3. In the later materials earthworms were active for an additional 1.5 months.

A 2-way ANOVA (factors: plant species and stage of decomposition) showed that absolute growth rates of earthworms during period 1 increased significantly ($p < 0.05$) in the order:


mass [mg]
600
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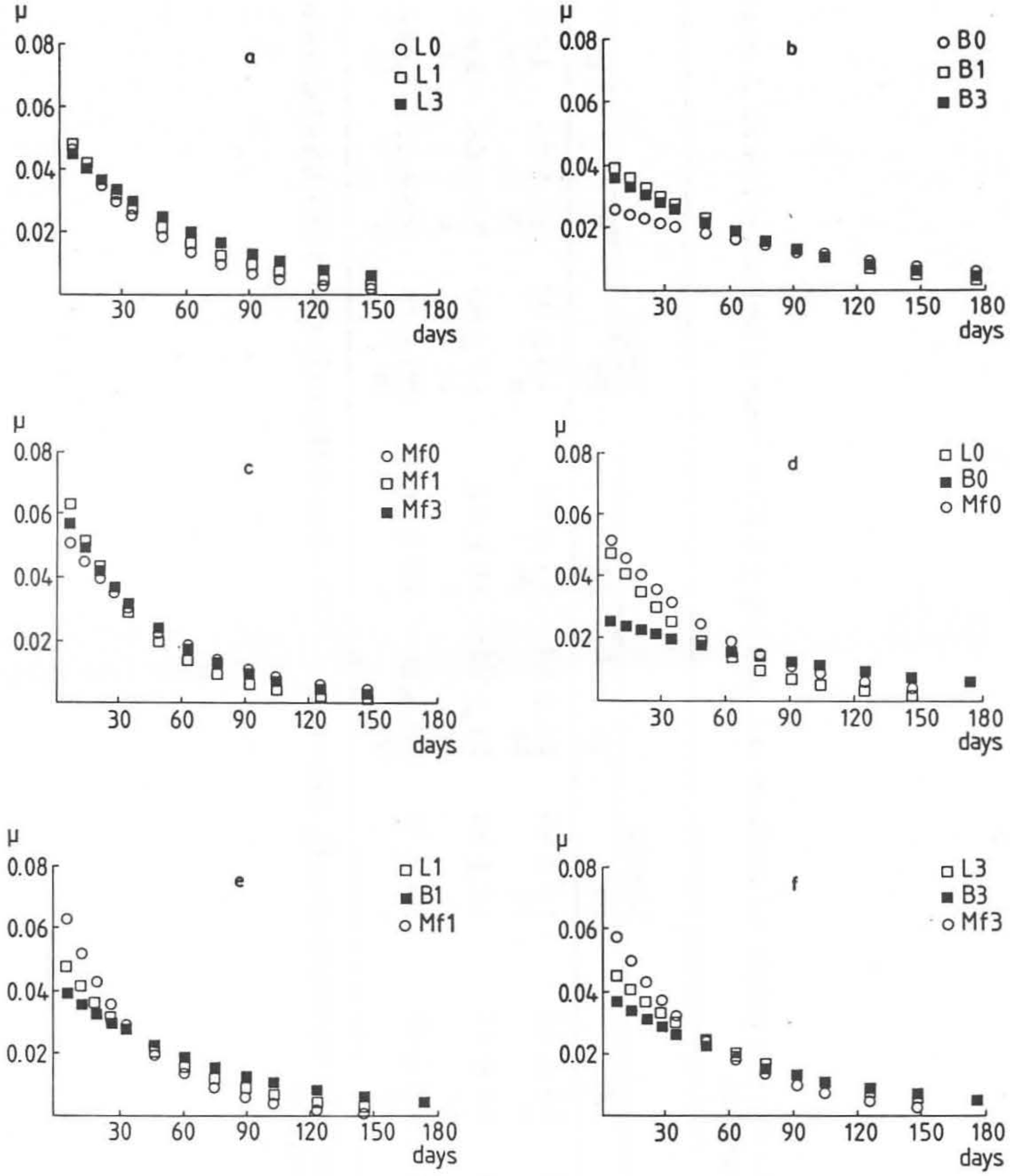

Fig. 2. The change of the specific growth rate with time for juvenile *A. caliginosa* according to the equation $\mu = \mu_0 \cdot e^{-Dt}$. The earthworms were grown in soil mixed with various plant materials. The materials were undecomposed or had been buried in soil outdoors. 0, 1 or 3 indicates the number of months plant materials were below ground. Comparisons between materials of the same species (a—c) and stage of decomposition (d—f).

Fig. 1. Mass of juvenile *A. caliginosa* expressed as the mean of four to five earthworms (mg ± S.E.) fitted to a Gompertz growth equation. The earthworms were grown in soil mixed with 2 g of a) meadow fescue (Mf), b) lucerne (L) or c) barley (B). The materials were undecomposed or had been buried in soil outdoors. 0, 1 or 3 indicates the number of months plant materials were below ground.

Table 3. Absolute growth rate (mg day^{-1} ± S.E.) for two time periods and maximum mass gain (mg ± S.E.) as means of four to five juvenile *A. caliginosa* fed 2 g of plant material in various stages of decomposition

	Materials[1]) Meadow fescue			Lucerne			Barley		
	Mf0	Mf1	Mf3	L0	L1	L3	B0	B1	B3
Period 1 (day 1—64)	3.2 ± 0.3 a	3.4 ± 0.4 a	3.2 ± 0.3 a	1.7 ± 0.3 cd	2.2 ± 0.2 bc	2.7 ± 0.2 ab	1.0 ± 0.1 d	2.1 ± 0.1 bc	1.8 ± 0.4 cd
Period 2 (day 64—127)	3.8 ± 0.4 a	1.4 ± 0.9 c	3.2 ± 0.7 ab	1.4 ± 0.6 c	2.4 ± 0.2 abc	3.6 ± 0.2 a	1.8 ± 0.1 bc	3.6 ± 0.4 a	2.8 ± 0.3 abc
Maximum mass gain	494 ± 46 a	377 ± 47 bcd	450 ± 60 abc	264 ± 30 e	350 ± 21 cde	498 ± 21 a	301 ± 13 de	510 ± 29 a	484 ± 27 ab

Note: Means in the same row followed by the same letter are not significantly different ($p > 0.05$), t-test (LSD) made after ANOVA (factor: material). The SAS procedure GLM (SAS Institute Inc. 1982) was used.

[1]) Explanation of symbols see Table 1.

barley $<$ lucerne $<$ meadow fescue, and that growth rates were lower in undecomposed materials than in materials which had been buried in the soil. For growth rates during period 2 and maximum mass gain the 2-way ANOVA indicated interactions between the factors. Therefore, the data were analysed in a one-way ANOVA with the nine plant materials as the factor (Table 3). During period 2 the earthworm growth rate was lower in Mf1 ($p < 0.05$) than in other fescue material which resulted in a low maximum mass gain (Table 3). Earthworms grew slower in L0 than in L3 ($p < 0.05$) and the maximum mass gain was lower in L0 ($p < 0.001$) and in L1 ($p < 0.05$) than in L3. The growth rate in B0 was only about half of that in B1 ($p < 0.05$) and worms growing in B0 showed lower maximum mass gain than worms in B1 or B3 ($p < 0.001$ and $p < 0.01$, respectively).

Comparisons among undecomposed materials reveal that earthworms grew most rapidly and reached highest masses in fescue ($p < 0.05$). During period 2 the growth was slower in Mf1 than in B1 ($p < 0.05$) and the latter material promoted the highest maximum mass gain. All materials which had been below ground 3 months produced the same maximum mass gain.

Materials from the same plant species, irrespective of decomposition stage, produced similar changes in the relative growth rates with time (fig. 2a—c). For each decomposition stage, meadow fescue gave the highest relative growth rates and barley the lowest during the first part of the study, while the relationship was reversed during the later part (fig. 2d—f). Initially high relative growth rates were followed by a faster decrease than initially low growth rates.

Although the experiment was not specifically designed for a regression analysis, the method was considered helpful for indicating the influence of food qualities on earthworm growth. The SAS procedure STEPWISE (SAS Institute Inc. 1982) indicated that high nitrogen content and a high proportion large (>0.5 mm) particles in the plant materials significantly ($p < 0.001$) decreased the earthworms growth rate during period 1. Growth rates were not significantly influenced by the carbon content or the particle length. The C/N-ratio was omitted from the analysis since it was closely correlated with the nitrogen content. According to the same method, the analysed properties did not significantly influence maximum mass gain or the growth rates during period 2.

4. Discussion

4.1. Concentration of organic matter in the soil

Juvenile *A. caliginosa* cultured in the same soil as that used in this study but with all visible organic matter removed, grew extremely slowly. After 157 days the mass increase was only 36 mg juvenile^{-1} (Boström & Lofs-Holmin 1986), i.e., only 14% of that in L0. Furthermore, earthworm growth in soil mixed with 1 g undecomposed plant material was studied. By assuming that all material was consumed when worms reached maximum mass, earthworm growth promoted per unit food can be calculated. Although aestivating worms were excluded in the previous study, lucerne and meadow fescue promoted 5% and 25% lower earthworm masses per gram material, respectively, than in this study. Thus, earthworm growth per gram food increased in soil with a higher concentration of plant material.

4.2. Earthworm activity

The earthworms were active for a longer time in barley than in the other materials. During early stages of decomposition, plant materials high in nitrogen and low in lignin decompose more rapidly than materials low in nitrogen and high in lignin (Tenney & Waksman 1929, Zieliński 1980) and the rate of decomposition is more rapid in materials with initially low C/N ratios (Doughty 1941). Barley straw contains about 20% lignin while the content in lucerne and meadow fescue is below 10% (Theander & Åman 1978, Whitehead 1972a, b). Thus barley should decompose most slowly (Table 1) which may prolong the earthworm activity.

Doeksen (1964) found that diapause was induced when *A. caliginosa* was added to soil earlier conditioned by the same species. Worms died or entered diapause also when the conditioned soil had been mixed with equal amount of fresh soil. In the present study worms lost mass or entered aestivation after approximately 5 months. The reason for this could be food deficit but it could also be due to toxic substances excreted by the worms themselves as reported by Doeksen (1964).

Since 2 of the earthworms in Mf1 entered aestivation very early, absolute growth rate during period 2 was lower in Mf1 than in other fescue materials. Although food shortage or toxic casts could have induced the early aestivation, the cause could not be definitely established.

4.3. Nitrogen

Nitrogen concentration increased and C/N ratio decreased in barley and meadow fescue during decomposition. This has earlier been observed for other plant materials low in protein such as wheat and rye straw (Tenney & Waksman 1929, Brown & Dickey 1970, Smith & Douglas 1971). When the initial material contained large quantities of nitrogen and decomposed rapidly the nitrogen concentration decreased during the early decomposition stages (Tenney & Waksman 1929). In the present study the nitrogen concentration decreased in the protein-rich lucerne during the below-ground period.

Abbott & Parker (1981) reported that the earthworm *Eisenia fetida* Sav. lost mass on a nitrogen-poor diet. Barley (1959), on the other hand, did not conclude that worms gain mass more rapidly on nitrogen-rich food although earthworm growth increased with increasing nitrogen concentration. The various foods also differed in many other qualities. The regression analysis in the present study indicated that high nitrogen concentration decreased earthworm growth rate during the first two months. The increasing nitrogen concentration in meadow fescue during decomposition was not associated with a corresponding decrease in earthworm mass, and the worms reached higher masses in L3 than in Mf1, despite similar initial concentrations of nitrogen in the materials. Earthworms fed B1 and B3, showed mass gains similar to worms fed Mf0 and Mf3, despite the difference in C/N ratios between the substrates. Thus, no clear relationship between food nitrogen concentration and earthworm growth was found in this study.

4.4. Particle size

The plant materials were ground in an attempt to simulate field conditions under which organic matter is mechanically broken up by biological and abiotic processes in combination with soil cultivation. The grinding also enabled similar preparations of replicates. The particles formed when the plant materials were ground varied in size and shape. When the gut contents of adult *A. caliginosa* were examined, Piearce (1978) did not find any mineral particles longer than 0.76 mm or wider than 0.55 mm and the maximum particle size for identifiable organic fragments was 3.00 mm × 0.37 mm. The largest mineral particles found in juvenile individuals were 0.2 mm (Bolton & Phillipson 1976). Possibly, the capability of worms to utilize nutrients in the ingested food varies with particle size. It has been found that earthworms grow more per unit food when fed finely ground organic matter than when the food contains large particles (Neuhauser *et al.* 1980a, Boström & Lofs-Holmin 1986).

Since the meadow fescue material mainly consisted of leaves, while lucerne and barley were mostly stems and straw, the particles in the former material became thinner when ground. The particles became shorter in more decomposed materials, thus giving rise to larger particle surface areas accessible to microorganisms. The earthworms grew well on Mf0 or Mf3 and when fed barley or lucerne the worms grew better on partly decomposed material which contained more small particles. Although it is difficult to discriminate between individual components, this indicates that particle size is a most important factor influencing earthworm growth.

4.5. Toxic substances in the lucerne

The mass increase of *A. caliginosa* in L0 was relatively poor even though the material contained more nitrogen and more small particles than B1, which constituted an excellent food. One explanation could be that earthworms are susceptible to certain substances in the lucerne, as have been found for other materials. A commonly occurring leaf polyphenol, catechin, is repellent to *L. terrestris* and palatability of oak litter increases after weathering, probably resulting from the breakdown of polyphenolic substances (SATCHELL 1967). A culture medium consisting of a fresh mixture of lucerne and soil is highly toxic to juvenile *A. caliginosa* [BOSTRÖM & LOFS-HOLMIN 1986]. Neither nitrate, nitrite nor ammonium seemed to have been the substance responsible for the toxic effects. The toxicity disappears when the mixture has aged for 14 days, i.e., when worms are added they do not die or enter aestivation. Lucerne tops and roots contain saponins (MORRIS *et al.* 1961), which are toxic to animals with external permeable surfaces, such as snails and fish (EWART 1931). Possibly these or some other substances present in the lucerne or formed by microorganisms may retard earthworm growth in undecomposed material. This could also partly explain why no clear connection between nitrogen content in the substrate and worm growth was found in the present study.

4.6. Growth rate

In the field there is a more or less continuous supply to the soil of dead organic matter which is consumed by earthworms, other soil fauna, and microorganisms. Hence, not only the maximum mass increase per unit food but also how fast the worms add mass is of interest when comparing nutritive values of plant materials. Materials in the present study which produced high earthworm masses also produced high absolute growth rates and vice-versa (Table 3). The absolute growth rate was considered useful for comparing the effects of different plant materials, although it is understood that growth in most cases is a non-linear process.

Juvenile *Eisenia fetida* SAV. was found to exhibit a growth pattern which follows the logistic curve of Verhulst (NEUHAUSER *et al.* 1980b). Due to disagreement in position of the inflexion point between the logistic growth curve and the growth curves in this study, the Gompertz equation was found more suitable to describe earthworm growth and fitted the data well (Fig. 1). This equation is derived by assuming that the substrate is non-limiting for growth but that the effectiveness of processes leading to mass increase decreases with time (FRANCE & THORNLEY 1984). This decrease can be viewed as being due to, e.g., differentiation or to senescence.

Although no statistical analyses were made on parameters derived from the Gompertz equation, it is indicated that the relative growth rate decreased faster with time when the initial value was high (Fig. 2a—f). This could be due to, e.g., a faster decrease of food supply or a with increasing mass inferior utilization of food nutrition for growth. Because individual growth is only temporarily exponential, growth rate should decrease as adult mass is approached. A faster initial mass increase may be accompanied by an earlier translocation of energy from growth to, e.g., development of internal organs.

The concentration of water solubles in barley straw buried in an unfertilized field plot decreased to one half within three weeks and the level was maintained fairly constant for two years (WESSÉN & BERG 1986). Hence, due to the 2 week incubation period this fraction should be similar in all plant materials with the same origin, irrespective of decomposition stage. This may partly explain the similarity concerning changes in the relative growth rate with time, observed for materials from the same plant species (Fig. 2a—c). The concentration of water solubles in barley is 4.9% which is considerably lower than in meadow fescue or lucerne, 28% and 34%, respectively (WESSÉN & BERG 1986, ANDRÉN, in press).

4.7. Selection of food

Earthworm casts usually contain higher concentrations of nutrients than the surrounding soil (LUNT & JACOBSON 1944, GRAFF 1971). If the decomposition of C is not extremely rapid during the passage through the gut, this shows that earthworms feed selectively on nutrient-rich matter in the soil. This study indicates that all 3 crop types can sustain the same earthworm growth per unit plant material provided the earthworms are able to select materials in adequate stage of decomposition.

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Synopsis: *Original scientific paper*

Boström, U., 1987. Growth of earthworms *(Allolobophora caliginosa)* in soil mixed with either barley, lucerne or meadow fescue at various stages of decomposition. Pedobiologia **30**, 5, 311—321.

The growth of juvenile *A. caliginosa* in soil mixed with 2 g meadow fescue, lucerne or barley was measured. The plant materials were initially undecomposed or had been buried in soil outdoors for one or 3 months. Individual earthworms were weighed regularly until most of the worms in a treatment had entered aestivation. During the first 2 months the absolute growth rates of earthworms increased in the order barley < lucerne < meadow fescue, and the growth rates were lower in initially undecomposed plant materials than in materials which had been buried in the soil. Among undecomposed materials, earthworms grew significantly more on meadow fescue than on barley or lucerne. The earthworms reached similar masses in all materials which had been buried in the soil for three months.

No clear relationship was found between the nitrogen content in the food and the growth rate. However, it was indicated that a large proportion of small particles in the food increased the growth.

Key words: earthworms, growth, lucerne, meadow fescue, barley, decomposition.